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COMPARATIVE CRANIOLOGY OF RECENT REPRESENTATIVES OF THE GENUS BISON

By C. C. Flerov

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COMPARATIVE CRANIOLOGY OF RECENT REPRESENTATIVES OF THE GENUS BISON.

By C.C. Flerov

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The comparative craniology of the genus Bison has hitherto remained completely undeveloped; a myth has persisted to the effect that it is impossible to distinguish such clearly defined species as the aurochs and the bison by their skulls. This article contains the results of a study of the comparative morphology of the skulls of recent representatives of this genus and attempts a functional analysis. For this purpose we used the most varied collection of aurochs and bisons in various scientific institutions in the USSR[1], embracing a total of more than 300 specimens of different age and sex.

The data we obtained not only indicated sharp differences between both of these species and even subspecies, but also permitted us to describe all of these differences in relation to their adaptive trend.

The research was based on the skulls of adult males. Some features of females were less clearly defined than others. An analysis of the skulls of calves up to the age of one year will be given in a special study.

The Aurochs Bison bonasus (Linnaeus)

Description. Skull (see figs. 1, 2 and 3). Relatively small to large sizes (for Bison). Greatest length, 490 to 580 mm; average, 525 mm; width behind orbits, 220 to 285 mm; average, 255 mm; width along rear walls of orbits, 290 to 350 mm; average, 320 mm. The skull is comparatively short and narrow in the frontal portion. The facial section is shortened. The forward ends of the intermaxillare either have no projecting blades on the forward outer edge or are very small. The muzzle becomes narrow and rounded towards the front. This results from the form of the incisors of the lower jaw and the manner in which forage is bitten off.

The aurochs feeds on arboreal forage or soft, lush forest grasses; its system of incisors is only slightly expanded and chisel-shaped, and therefore the antagonists of the incisors--the intermaxillary bones (a soft pad) --are not expanded. Male and female structures are equal. The palatine processes of the intermaxillare are wide as far as their forward edge; the vomer are thin and flat (as in Bison Bonasus bonasus) or are bent in longitudinally, forming a broad groove (as in Bison bonasus caucasicus)*. The nasal bones are broad, short, and oval. They are widest in the middle.

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1 The main collections are kept at the Zoological Institute of the Academy of Sciences, USSR, at Leningrad, in the Zoological Museum of Moscow University, and in other institutes and museums.

* In the Russian this sentence is ambiguous because of missing punctuation. A possible variant is: "The palatine processes of the intermaxillare are wide as far as the forward edge of the vomer; they are thin and flat....."

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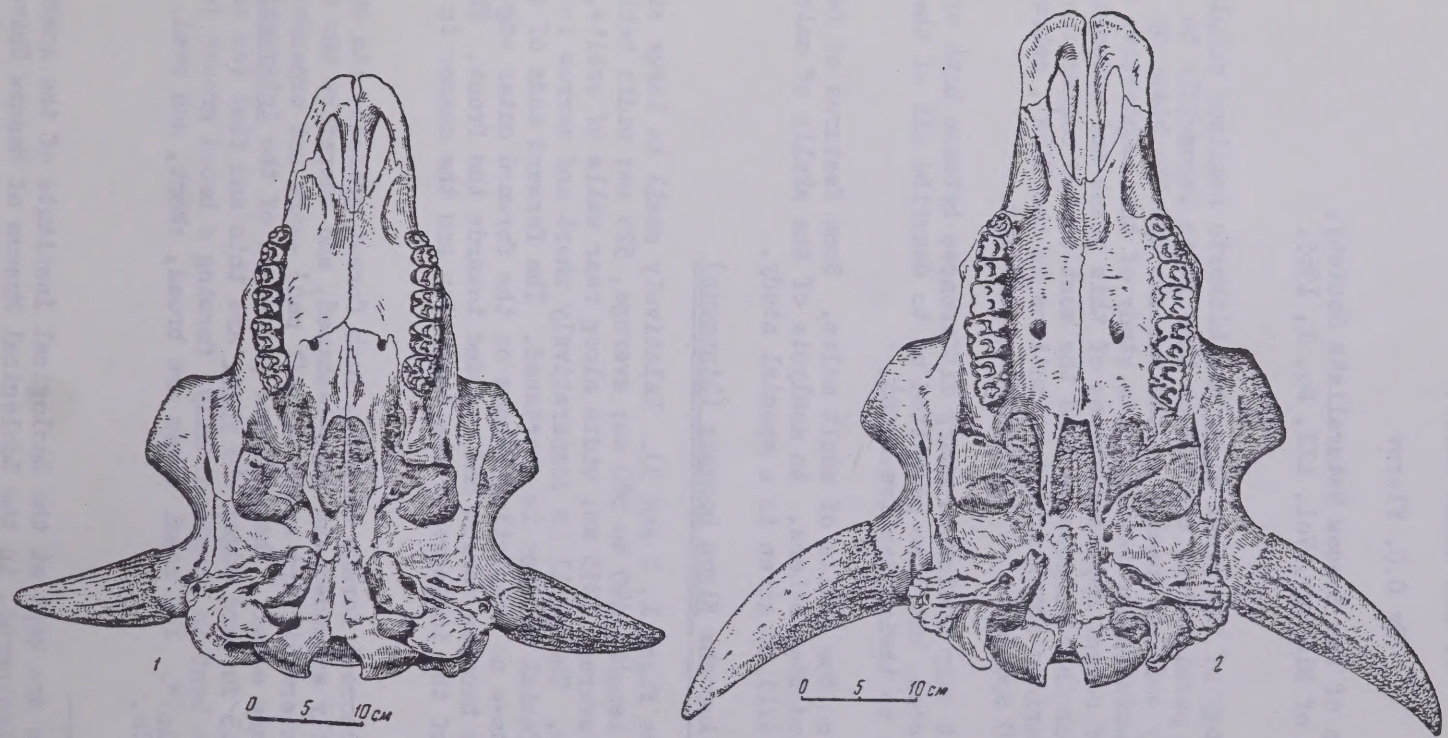

Fig. 1.

Skulls: 1 - aurochs (Bison bonasus);

2 - bison (Bison bison), from below

There are numerous depressions and protuberances on the forehead. One depression between the orbital cavities and immediately behind the nasal bones is a constant feature; a second depression is consistently located at the rear end of the frontal bones in front of the parietal [bone]; two depressions (the lateral cavities) approximately at the level of the forward edges of the horn shafts along the sides (on the right and on the left) are occasionally very vaguely distinguished from the central frontal prominence. There are no impressions above the orbits in front, in the region of the forward third of the sulcus supraorbitalis, or along the sides of the rear ends of the nasalia. Depressions on the skulls of aurochs result from poorly developed frontal cavities, while the absence of such depressions on bison is explained by well developed frontal cavities. The bison's head is larger than that of the aurochs; the frontal bones are thicker, necissitating reduced head weight, achieved by well developed frontal cavities.

The horn shafts project almost straight out at the sides and only slightly backwards. Their ends lie in front of the rear edge of the skull. The shafts are long both absolutely and relatively; the distance between their ends varies from 525 to 690 mm and averages 610 mm. The shafts are not bent downwards beneath the frontal surface and their ends point upwards.

The direction of the horn shafts depends upon the general biomechanics of the skull, and in particular on the lines of force of the frontal-nasal region (the width and convexity of the forehead), the extent to which the portions of the frontal surface preceding the horns are raised, and so on. Therefore, on B. bonasus the horn shafts are not thrown down and back, as is the case with B. bison. In general, the extent to which the horns are recurved down and back is related entirely to the width and convexity of the forehead. On species with the widest and most convex foreheads (bison and buffalo), the horns are bent back and down and, conversely, on species with narrow, flat, and even depressed foreheads (the goat and the yak), the horns point up and forwards. Generally speaking, the aurochs has a narrower and less convex forehead than the bison, and its frontal bones are less massive; the horns of the aurochs are therefore not "set" as far back as those of the bison. This is clearly visible even on different skulls of one and the same species: on specimens with broader, more convex foreheads, the horns are more recurved than on specimens with narrow foreheads. In Caucasian aurochs, the forehead is slightly convex and the horns are bent more than is the case with Bialowieza Forest aurochs.

The shafts are broad at the base; the diameter of a shaft at the crown varies from 65 to 90 mm and averages 80 mm.

The bases of the horn shafts are not prolapsed; hence the distance between them and the external auditory opening is extensive and is much greater than the vertical diameter of the foramen magnum. The horns are bent in a sharp spiral: to the sides and forward, then up, back, and in. The horn shafts of females are rounded in section and, in males, somewhat flattened. The forward - rear diameter is greater than the vertical diameter[2].

The sulcus supraorbitalis is broad, in the form of a clearly outlined, deep, wide groove with numerous openings and branchings onto the orbital "socket" and the frontal surface. The sulcus does not ossify and remains open for the entire life of the animal. There may occasionally be a slight ossification in the rear portion behind the foramen supraorbitale in very old specimens. The lateral

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2 A feature peculiar to all representatives of the genus Bison.

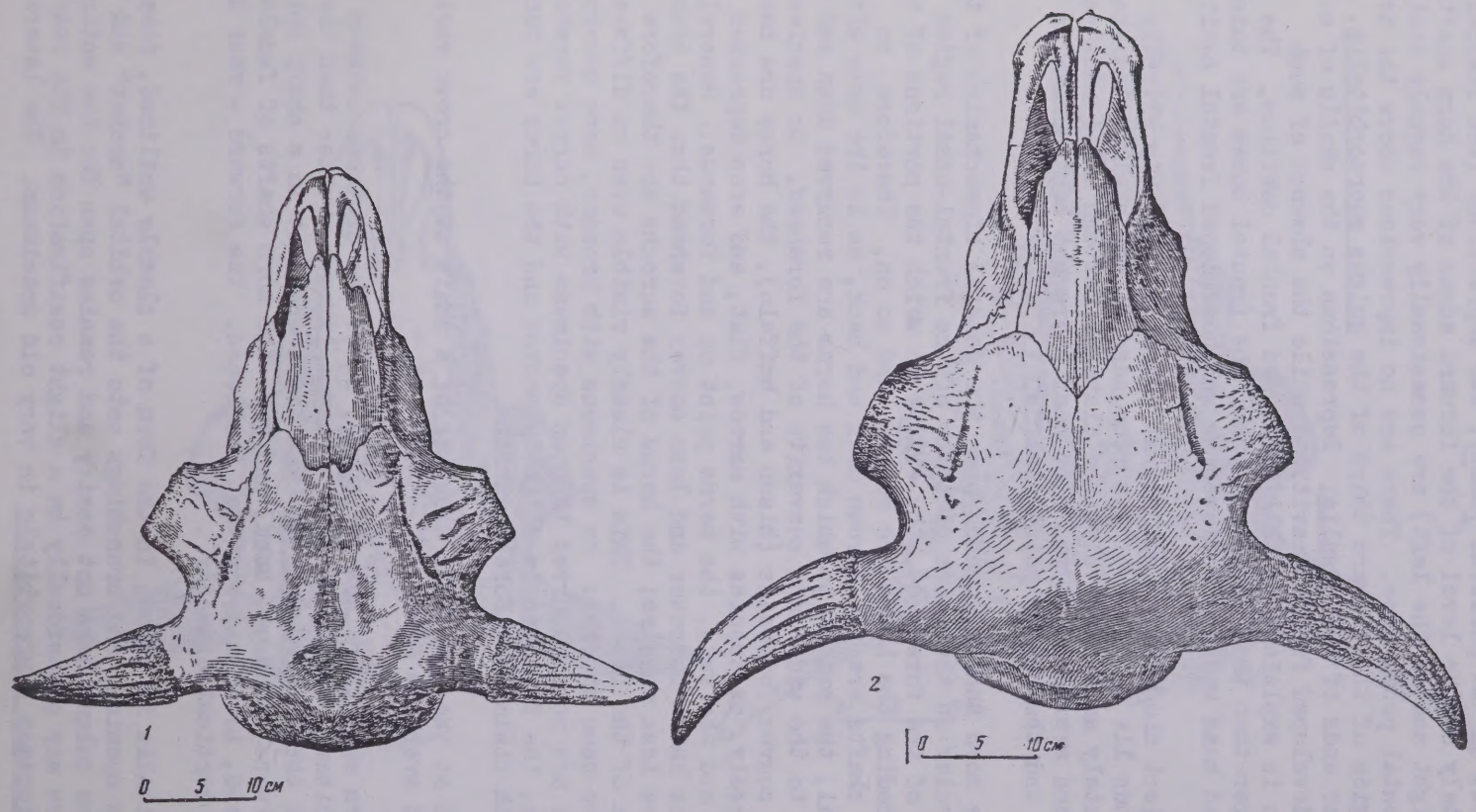

Fig. 2.

Skulls: 1 - of aurochs (Bison bonasus)

2 - of bison (Bison bison), from above

branches of the sulcus never ossify. In females the sulcus is broad and continues forward as far as the seam with the oslacrymale. The foramen supraorbitale is almost always open on top.

The orbits are directed slightly to the sides and forwards. The lacrymal bones are narrow; they always have a recess in front and, in most cases, form a narrow isolated spur wedged in between the nasal and upper maxillary bones. There is a broad preorbital depression in the region of the forward portions of the lacrymal bones, resulting from the greater development of the muscles moving the upper lip (musculus levator nasolabialis) and its great mobility when the animal feeds on arboreal forage. In females this depression is not as pronounced as in males.

The facial portion of the skull (in the region of the ossa maxillaria) is low and the distance from the lower edge of the orbit to the edge of the alveolus of M^3 is much less than the length of the molars and premolars. Hence the nasal plate of the os maxillare is low, while the forward portion of the cheekbone is narrow. The facial section of the skull is comparatively wide; its width over the forward edge of M^3 exceeds the length of a row of premolars and molars.

The choana is low and the pterygoid processes are short. The nasal cavity is of moderate size, like the ventral nasal passage and the naso turbinalia. The moderate volume of the nasal cavity, as compared with that of B. bison, is evidently explained by a reduced need for warming air inhaled in winter. In the forests the animals have no occasion to cross extended open areas in cold wind and rarely move at a swift gait. Since the choana is low, the edges of the allae magnae are also low. They are recurved outward and have no dorsoventral depression bounded by crests. The edge of the ascending branch of the lower jaw from the processus angularis to the processus condyloideus is short. The area where the medial layer of the musculus pterygoideus is attached is small; the layer itself is narrow and comparatively delicate. The lower jaw, therefore, has comparatively little capacity for moving forward and its forward and backward movements are limited. The processus angularis of the lower jaw is low, hence the lateral layer of the musculus pterygoideus is also delicate. The area of attachment of the musculus masseter is of moderate size as a result of the low height of the os maxillare and the short distance from the tuber malare to the rear end of the jugale (less than 200 mm). The tuber malare is weak and does not form a projecting process. On the outer edge of the zygomatic arch, on the ventral side, and only on the jugale, there is a weakly defined crest, which does not continue through to the processus zygomaticus ossis temporalis. The inner edge of the zygomatic arch has no crest; hence its ventral side is flat and has no longitudinal impression. Because of the relatively small size of this muscle, its comparative weakness, and the limited extent to which it is permeated with tendons, the surface of the area in which it is attached to the os maxillare and to the ventral side of the zygomatic arch is more or less smooth and almost free from grooves and ridges[3]. Since the facial section of the skull is low, the brain section depressed and the processus paroccipitalis directed downwards, the latter's lower terminals are approximately at the level of the palate. The parietal region and the entire occiput are prolapsed below the forehead; hence the parietal bones are directed

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[3] All of these features are even less clearly defined in B. bonasus caucasicus than in B. bonasus bonasus because of softer food and a very low os maxillare.

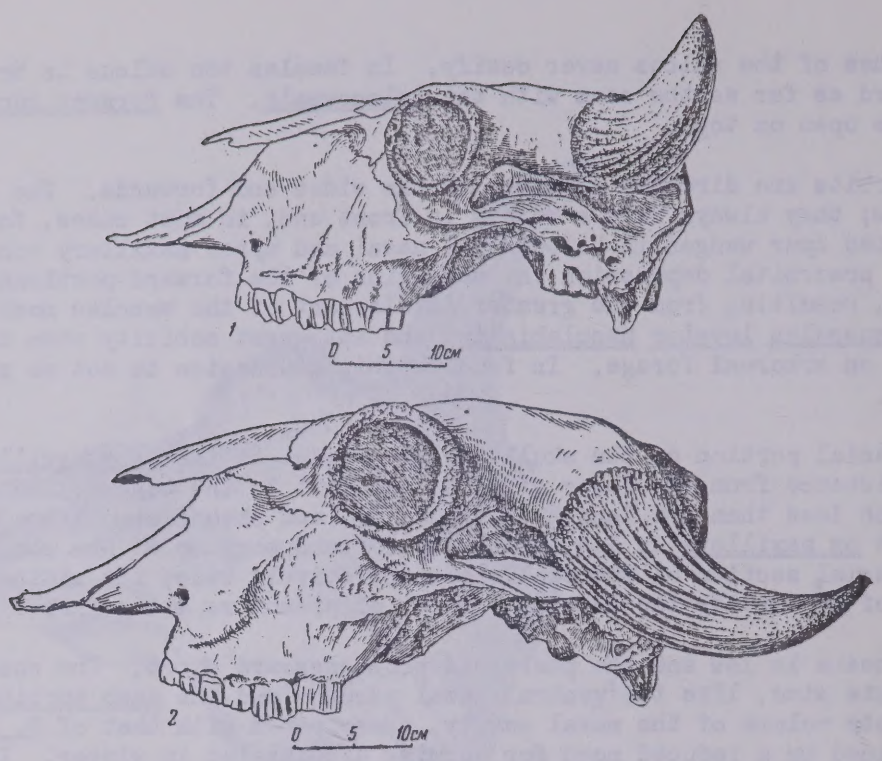

Fig. 3.

Skulls: 1 - of an aurochs (Bison bonasus);
2 - of a bison (Bison bison), from the side.

upwards and to the rear at an angle of approximately 130° to the longitudinal axis of the skull (a feature distinguishing this species from the ancient Asiatic and European B. cesaris). The upper edge of the occipital crest is always noticeably lower than the base of the horn shafts. The opening of the meatus acusticus externus is low, much lower than the level of the seam between the os jugale and the os maxillare. The occiput is narrow (the crests are small as a result of the comparatively light weight of the head); its greatest width (in the region of the outer auditory openings) is approximately twice the distance from the upper edge of the foramen magnum to the upper edge of the occipital crest. The distance from the external edges of the condyles to the lateral edge of the occipital crest above the meatus acusticus externus is much less than the length of $M^2 + M^3$.

The occipital condyles (see fig. 4) are either rounded on their external edges at the base or have a rudimentary hook-shaped bend forward. Their forward edges are extended apart on the pars basilaris ossis occipitalis (in front of the foramen magnum). The distance between them is approximately 12 mm.

The basioccipitale is shortened and gradually narrows towards the front. Its width in the region of the pharyngeal protuberances is usally much less than the length of $P^3 + P^4$. The pharyngeal protuberances are short and narrow, but at the same time are high and project noticeably downwards in the form of hook-shaped processes. They are drawn back and, because of the shortness of the basioccipitale, lie far behind the rear edges of the allae magnae and the rear

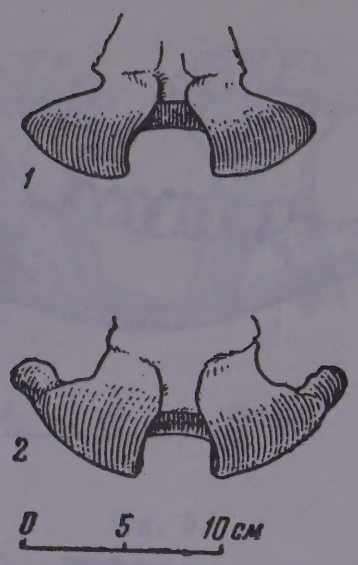

Fig. 4.

Condyles: 1 - of an aurochs (Bison bonasus);
2 - of a bison (Bison bison).

edge of the choana. The limited tuberculum pharyngeum indicate [sic] a relatively weak development of the musculus longus capitis, explained by the fact that the aurochs, which feeds more on arboreal forage, lowers its light head comparatively rarely[4].

The articular surfaces for the pulley of the lower jaw are short and their area comparatively small. The length from the articular process to the forward edge is less than that of $P^3 + P^4$. The postarticular process is low; its height is less than the length of P^3. The opening of the temporal canal is situated on a level with the protuberance of the articular surface. The weak development of the articular process is explained by the extent to which the motions of the lower jaw are limited when soft foods are being ground: movement is almost exclusively lateral, while backward and forward motions are limited. The articular protuberance is convex; the transverse groove between it and the postarticular process is bent in the shape of a sickle. This, together with the sickle-shaped bending of the articular pulley of the lower jaw, indicates the presence of rotary, transverse movements characteristic of the lateral grinding motions of the lower jaw. This structure is equally common to males and females.

The eardrums are large and highly distended; the tympanohyale is located in the middle, and the external and internal parts of the drum are approximately equal. The internal portion of the eardrums between the tympanohyale and the

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4 In comparison with B. bison.

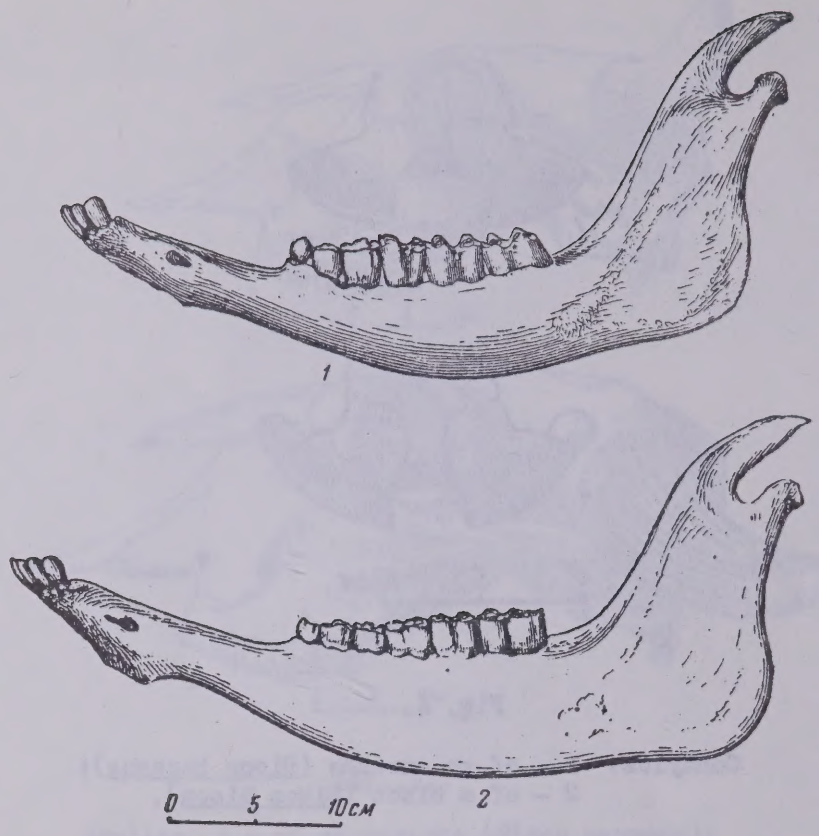

Fig. 5.

Lower jaws: 1 - of an aurochs (Bison bonasus);
2 - of a bison (B. bison bison).

basioccipitale is large and distended; the forward end of [each] drum is wide and distended with several acuminate processes. The drums are of equal height along their entire length; there are three or four distended protuberances on the lower surface that projects from the body of the skull. The forward ends of the drums lie in front of or on a level with the middle of the pharyngeal protuberances. The external auditory canals are short; the distance from the bullae to the edge of the meatus acusticus externus is less than or, less frequently, equal to the length of the bullae themselves. The processus par paroccipitalis are [sic] directed sharply downwards and somewhat inwards; their ends project down far below the surface of the basioccipitale. They are connivent, and the distance between their ends is less than the height of the occiput from the upper edge of the foramen magnum to the top of the occipital crest.

The choana is wide and its pterygoids are outspread. The width of the choana in front of the palate is equal to the length of M^2. The greatest width of the entry exceeds considerably the length of $P^2 + P^3$. Structure is equal in males and females.

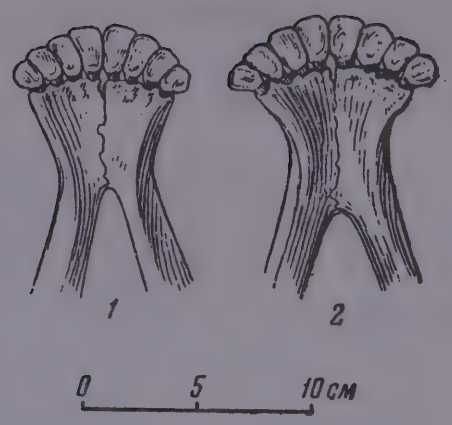

Fig. 6.

Forward section of lower jaw:
1 - of an aurochs (Bison bonasus);
2 - of a bison (Bison bison).

Lower jaw (see figs. 5 and 6). The branches of the lower jaw (pars dentalis) are low; their height, on the level of M_3, is equal to the length of $M_1 + M_2$; they are comparatively heavy and distended. The pressure achieved by chewing with the lower molars is comparatively weak as a result of soft foods. The movements of the lower jaw, when food is being ground, are mainly lateral. The pars dentalis is therefore low, but the internal portion of its body is thickened longitudinally on the level of the alveolus; further down, however, the jaw becomes thinner. This structure has resulted from pressure in a substantially medial direction.

The articular process (processus condyloideus) is wide and long, less than twice as wide as it is long. It is rounded in the rear. The forward section of the lower jaw in the region of the symphysis is low and rounded from the bottom. The incisor portion widens gradually and has no sharply protruding angles because of the relatively narrow system of incisor - like teeth directed forwards and slightly to the sides. The symphysis is short in males and females; its length is less than that of $M_2 + M_3$.

Teeth. M_3 has a small, slightly isolated talonid, which is frequently recurved outwards to the level of the outer layers of the main tooth columns. Occasionally the talonid is reduced. The forward internal fold M_3 is slightly separated from the forward column of the tooth. A vertical groove, separating this fold from the forward column, is missing from the lingual side in the forward portion of the tooth. The depressions between the columns of the lower molar teeth are small on the lateral and lingual sides; the columns, therefore, are only comparatively slightly separated. The width of the teeth along the columns is much less than twice their width along the depressions between the columns. The incisors are comparatively slightly recurved outwards and, in general, form a chisel-shaped system for cutting bark and branches that is narrower than that in Bison bison but which is nonetheless capable of sustaining considerable pressure.

The Bialowieza or Lithuanian Aurochs Bison bonasus bonasus (Linnaeus, 1758)

Type. Unknown. Described by Linnaeus probably on the basis of specimens from the Bialowieza Forest.

Description. The skull is comparatively large for Bison bonasus. The overall length is 500 to 580 mm; the width of the forehead is least behind the orbits (220 to 285 mm). The forehead is convex; the distensions at the base of the horn shafts are not clearly noticeable. The preorbital pit is wide and less clearly defined than in B. bonasus caucasicus. The condyles are rounded ouside and do not have the rudiments of a forward bend. The nasal cavity is of moderate volume; the skull, therefore, is also of moderate height in the facial region and the distance from the lower edge of the orbit to the edge of the alveolus M^3 is approximately one-fourth of the length of a row of premolars and molars. The protuberance and ridge on the maxillare (tuber malare), like the attachment surface of the musculus masseter, are moderate.

The palatine processes of the intermaxillaria along the dorsal surface are almost flat; their upper processes (processus nasalis) are of moderate length and sharply acuminate, by no means reaching the nasalia. They always greatly exceed the length of M^1.

The horns of the cows are comparatively slightly bent inwards and their ends are far apart. The horns of the males are spiral: they point out, up, in, and slightly back. The horn shafts are directed to the sides and slightly back; the ends are bent upwards.

Caucasian Aurochs Bison bonasus caucasicus (Satunin 1904)

Type. Incomplete hide of an adult female. Zoological Institute of the Academy of Sciences, USSR, No. 22087, Collector: Baron Rozen, 1836. Obtained through Academician K.E. Ber. Northern Caucasus (northwestern).

Description. The smallest of all Bison. The skull is smaller than in B. bonasus bonasus. The overall length is 490 to 560 mm; the width of the forehead is least behind the orbits, where it measures from 220 to 250 mm.

The forehead is in most cases almost flat and very slightly convex; there are always two distensions at the base of the horn shafts. The pits and depressions in the forehead are well defined, as in B. bonasus bonasus.

The preorbital pit is clearly defined, while the upper edge of the lacrymal bone is in the form of a ridge and is set vertically. The condyles frequently have the rudiments of a forward bend.

The nasal cavity is comparatively very small; therefore the skull in the facial portion is low and the ossa maxillaria are also low. The distance from the lower edge of the orbit to the edge of the alveolus of M^3 is approximately one-third of

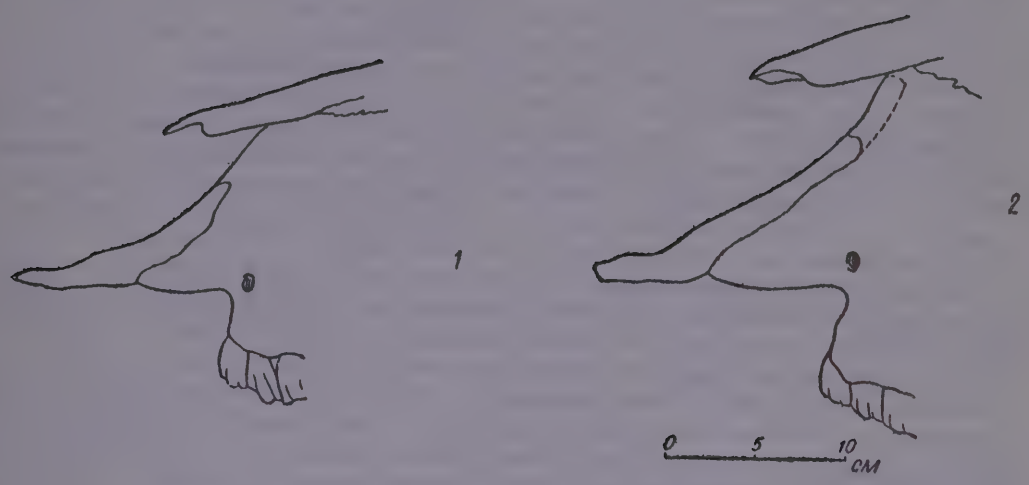

Fig. 7.

Intermaxillary bones: 1 - of a Bialowieza aurochs (B. bonasus bonasus);
2 - of a Caucasian aurochs (B. bonasus caucasicus).

the length of a row of premolars and molars. The small volume of the nasal cavity has resulted from the animal's having lived in a relatively warm climate, rarely run, and rarely inhaled cold air with any intensity. The protuberance and ridge on the maxillare (tuber malare) over M^{I} are weakly defined. The area of attachment of the musculus masseter is relatively small.

The palatine processes of the intermaxillare are bent in longitudinally along the dorsal surface; the bone is, in general, longer than in the Bialowieza varieties and its rear end (processus nasalis) terminates in most cases in a wide, blunt peak. The distance at which it approaches the nasalia is less than the length of M^{I}; occasionally, it comes into contact with the nasalia. The horns of cows are very noticeably bent inwards in such a way that their tips come very close together, frequently assymetrically. The horns of the male are sharply spiral (out, forward, up, in, and back); they are much stronger than those of the Bialowieza variety. The horn shafts are pointed straight out to the sides or even slightly forwards or barely backwards, while the tips are pointed upwards.

The Bison Bison bison (Linnaeus)

Description. Skull. Relatively large for bison. Its greatest length is from 490 to 600 mm, averaging 565 mm; the width behind the orbits is from 240 to 315 mm,

averaging 275 mm; the width along the rear walls of the orbits is from 270 to 385 mm, averaging 330 mm. The skull is relatively long and wide in the frontal portion. The facial section is elongated. The forward ends of the intermaxillare have projecting, blade-like protuberances on the forward outer edge. The muzzle is wide in front, peculiar to typical Pecor herbivores, whose entire system of incisors, which are widened and recurved outwards, has an enlarged common edge adapted for seizing and cutting large quantities of grass. The antagonists of the incisors - the intermaxillary bones - are therefore widened. Structure in males and females is equal. The palatine processes of the intermaxillare narrow sharply backwards towards the vomer; they are thick and their height increases towards the rear. A deep longitudinal groove is formed on the dorsal surface; there are also longitudinal grooves on the lateral surface, while the lower surface is flat. The nasal bones are comparatively long and narrow. They narrow to varying degrees in the shape of a wedge towards the front in such a way that their greatest width is on a level with the seam between the lacrymal and frontal bones. They are more clearly defined in females than in males. There are either no depressions on the forehead or they are weakly defined; the surface of the forehead is smooth and convex. In females the forehead is smooth. Small impressions are observed above the orbits in front, in the region of the forward third of the sulcus supraorbitalis, and along the sides of the rear ends of the nasalia. The horn shafts go out to the sides and back in such a way that their tips project noticeably back beyond the rear edge of the skull. The shafts, which change along their length, are short in B. bison bison; the distance between their tips is 485 to 665 mm, averaging 580mm; in B. bison athabascae they are long; the distance between their tips is 585 to 740 mm, averaging 665 mm. They are recurved downwards to a greater or less degree: in B. bison bison they are below the frontal surface, while in B. bison athabascae the tips are located above the frontal surface. The tips of the shafts are pointed back and up. The shafts themselves vary in thickness: in B. bison bison they are relatively thick at the base (their diameter at the crown is 65 to 95 mm, averaging 75 mm), while in B. bison athabascae they are very thick, with a diameter varying from 80 to 110 mm and averaging 95 mm. The bases of the horn shafts are prolapsed; hence the distance between them and the external auditory opening is very short, less than or equal to the vertical diameter of the foramen magnum (occasionally somewhat larger in B. bison athabascae).

The bend of the horns varies in both subspecies, but the spiral bend is always less marked than in B. bonasus. The sulcus supraorbitalis is comparatively weakly defined and is usually not complete over the entire orbit, but is frequently broken. The openings are small; if branchings occur, they are defined only on the "socket" of the orbit. The sulcus is shallow and frequently narrow. It is heavily ossified; hence it grows over in its rear portion and forms a closed canal for not less than one-third of its length. The foramen supraorbitale usually opens into the sulcus canal that is closed from the top, and not freely onto the frontal surface; it is not visible from above. The lateral branchings frequently ossify and can form small closed canals. In the female the sulcus is very narrow and is usually far from the lacrymal bone.

The orbits are pointed sharply to the sides and forward. The lacrymal bones vary in form: in B. bison bison they are broad, frequently without a recess in front, and have no isolated tooth. Occasionally, the bones are sinuate and bear a forward tooth-shaped process (as in B. bison athabascae). Neither males nor females have a preorbital depression. The motors of the upper lip are weaker than in B. bonasus; the mobility of the upper lip is less, since the animal feeds on grasses.

The facial portion of the skull (in the region of the ossa maxillaria) is high; the distance from the lower edge of the orbits to the edge of the alveolus M^3 is greater than the length of a row of molars and premolars. The nose plate of the os maxillare is therefore high, and the forward portion of the cheekbone is considerably broadened. The choana is high and the pterygoid processes are long. This is explained by the great volume of the nasal cavity, enlarged by the ventral nasal passage and the substantial dimensions of the nasoturbinalia. In general, the large volume of the nasal cavity, as compared with that of B. bonasus, has resulted from the breathing and warming of cold air in winter under severe northern conditions (as in the case of B. bison athabascae) or on open prairies, where the animals frequently move over considerable distances and at a swift gait (as in the case of B. bison bison).

The choana is high; therefore the edges of the allae magnae are also high. They are not recurved outwards and on the outside have a dorsoventral groove bounded by corrugated crests and forming solid bases for the attachment of muscles. The edge of the ascending branch of the lower jaw from the processus angularis to the processus condyloideus is long. The region where the lateral layer of the musculus pterygoideus is attached is large; the layer itself is broad and thick. The lower jaw, therefore, has a great capacity for forward movement, and substantial backward and forward grinding movements are possible. The processus angularis of the lower jaw is high; hence the medial layer of the musculus pterygoideus is also strong. The area of attachment of the musculus masseter is very broad because of the marked height of the nasal plate of the os maxillare and the considerable distance from the tuber malare to the rear end of the jugale (more than 200 mm.). The tuber malare is thick and strongly defined. Well-defined crests run along the outer and inner edges of the entire zygomatic arch on the ventral side, extending along the jugale and the processus zygomaticus ossis temporalis and reaching the aural margin. A longitudinal impression forms between these crests. Because of the great size and power of the musculus masseter and the fact that it is considerably permeated with tendons, the surface of the area where it is attached to the maxillary bone and to the zygomatic arch is covered with grooves and ridges.

Due to the considerable height of the facial section, and despite the extent to which the brain section is prolapsed and the jugular processes (processus paroccipitalis) directed downwards, the lower ends of these processes are situated considerably above the level of the palate. The parietal region and the entire occiput, just as in B. bonasus, as distinguished from B. cesaris, is usually prolapsed below the forehead (in B. bison bison); hence the parietal bones are directed upwards and to the rear at an approximate angle of 130° to the longitudinal axis of the skull. The upper edge of the occipital ridge is in most cases (in B. bison bison) situated appreciably below the level of the horn shafts. The meatus acusticus externus opens low, below the level of the seam between the os jugale and the os maxillare. The occiput is broad and its ridges, because of the considerable weight of the head, are very large. The greatest width of the occiput in the region of the external auditory openings is usually more than twice as great as the distance from the upper edge of the foramen magnum to the upper edge of the occipital ridge. The distance from the outer edges of the condyles to the outer edge of the occipital ridge above the meatus acusticus externus is somewhat less than the length of $M^2 + M^3$, or approximately equal to their length.

The occipital condyles are extended on their outer edges at the base and form a ridge bent forward in the shape of a hook. Their forward edges on the pars basilaris ossis occipitalis (in front of the foramen magnum) are widely separated (in B. bison bison); the distance between them is about 14 mm. Otherwise, (as in

B. bison athabascae) they approach to a distance of about 8 mm. The condyles in B. cesaris have the same structure, which may be attributed to a more marked fixation of a heavy head frequently lowered when grass is eaten.

The basioccipitale is long and narrows in the middle between the forward ends of the condyles and the tuberculum pharyngeum. It widens in the region of the tuberculum pharyngeum; here, its width is usually much in excess of the length of $P^3 + P^4$. The pharyngeal protuberances are wide, in the form of broad, corrugated distensions, and do not form hook-shaped processes. They are distended forward and lie immediately at the edges of the allae magnae directly at the rear edge of the choana or proceed forward into the choana. The broad tuberculum pharyngeum [sic] may be attributed to the extensive development of the musculus longus capitis, resulting from B. bison bison's frequent lowering, when feeding on steppe grasses, of a head heavier than that of the aurochs. On B. bison athabascae they*) are corrugated, very large and long, and form crests and processes which are distended forward; the [tubercula pharyngea] proceed into the choana much further than the allae magnae. The musculus longus capitis is very well developed, since both the head and horns are very heavy.

The articular surfaces of the lower jaw pulley are long and their area is considerabl large - much broader than in the aurochs. The distance from the articular process to the forward edge [of the lower jaw] is equal to the length of $P^3 + P^4$. The articular process is well defined and high; its height is equal to the length of P^3. The opening of the temporal canal is situated considerably below the surface of the articular protuberance and the entire articular surface. This type of structure permits not only lateral, but strong forward and backward movements of the lower jaw when coarse steppe grasses are being ground. In general, the structure of the articular surface is similar to that of the steppe herbivores Bovidae. The articular protuberance projects slightly; there is almost no groove between it and the postarticular process. Such a structure permits both lateral and forward and backward movements of the lower jaw. Structure is the same in males and in females.

The ear drums are small and are not distended; their internal portion between the tympanohyale and the basioccipitale is not distended and develops immediately into a plate with two processes. Along this plate runs a vertical ridge. Thus, the internal portion from the tympanohyale on is practically absent. On the lower surface of the drum, in the middle, there is one protuberance; the rear and forward portions of the drum are much lower. The forward ends of the drums lie behind the pharyngeal protuberances. The foregoing structure applies to males; in females the bullae are large, but nonetheless somewhat smaller than in the female aurochs.

The external auditory canals are short and the distance from the bullae to the edge of the meatus acusticus externus is approximately equal to or greater than the length of the bullae themselves. While the dimensions of the bullae are less than in B. bonasus, the relative length of the canal in the male is similar to that in the aurochs and steppe bison. B. bison athabascae has a longer canal, since the overall width of the occiput is greater.

The direction of the processus paroccipitalis is the same as in B. bonasus: noticeably downwards and somewhat inwards. In B. bison athabascae they [sic] are

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*) Translator's note: Presumably referring to the tuberculum pharyngeum above.

turned more markedly inwards than in B. cesaris.

The choana is narrow and the pterygoids are not recurved outwards. Their width in front at the palate is equal to the length of P^4. The greatest width of the entrance is equal to the length of $P^2 + P^3$. The choana is the same in females as in males.

Lower jaw. The branches of the lower jaw (pars dentalis) are eminent; their height at the level of M_3 considerably exceeds the length of $M_1 + M_2$ and is approximately equal to the length of $M_2 + M_3$; they are relatively flat and not distended. The premolars and molars exert considerable pressure when chewing as a result of the animal's feeding on coarse forage. The grinding process involves more or less marked forward and backward movements in addition to lateral movements. Because of this the pars dentalis is elevated; since the relatively medial pressure is weaker, it must sustain considerable pressure downwards. The longitudinal enlargement at the level of the alveolus is therefore much less clearly defined than in the aurochs.

The articular process (processus condyloideus) is transversely extended; it is approximately twice as wide as it is long. It is straight and sinuate behind. The forward section of the lower jaw is elevated in the region of the symphysis; a strongly projecting ridge runs along the seam below. The incisor portion is sharply widened in front, forming angles projecting noticeably outward, due to the relatively broad system of incisor-like teeth pointing forwards and sharply to the sides. The symphysis in females is long - usually longer than $M_2 + M_3$.

Teeth. M_3 has a structure similar to that of B. bonasus, but the forward internal fold of this tooth is more sharply isolated. On the lingual side, in the forward portion of the tooth, a well-defined vertical groove runs from the masticating surface to the root, separating this fold from the forward column of the tooth. The molar structure is similar to that in B. bonasus.

The incisors are relatively sharply recurved outwards and are widened; in general, they form a wider grass-cutting system in B. bison bison than in B. bonasus. B. bison athabascae has a narrower system.

The Steppe Bison Bison bison bison

(Linnaeus, 1758)

Type. Unkown. Described from central Kansas ("Quivira region"[5]).

Description. Skull. Large; the greatest length is 490 to 570 mm, and averages 540mm; the width of the forehead behind the orbits is 240 to 290 mm, averaging 265 mm. The width along the rear walls of the orbits is 270 to 345 mm, averaging 317 mm. The skull is relatively long and broad. The forward ends of the intermaxillaria, on their forward external edge, bear blade-shaped processes projecting outwards. The muzzle is widened in front. The nasal bones in most cases become narrow towards the front in the shape of a wedge; hence their forward section is always much narrower than the rear. There is ordinarily no depression on the forehead behind the nasal bones. The horn shafts are short; the distance

5) P. Herschkovitz. Proc. Biol. Soc. Washington, vol. 70, p. 31, 1957.

between their ends varies from 485 to 665 mm and averages 580 mm. They are sharply recurved downwards below the frontal surface. The shafts are thin at the base; their diameter at the crown varies from 65 to 95 mm and averages 75 mm. Their bases are prolapsed; hence the distance between them and the external auditory opening is usually less than the vertical diameter of the foramen magnum. The horns have almost no spiral bend; rather, they are bent in one plane.

The sulcus supraorbitalis is very weak and has almost no branchings. The lacrymal bones are broad and in most cases have no incisure in front. A preorbital depression never occurs. The pharyngeal protuberances are large and lie immediately behind the edges of the allae magnae but do not enter the choana. The choana is narrow and elevated. The forward ends of the occipital condyles are spread apart in front of the foramen magnum; the distance between them is about 14 mm.

The system of incisor-like teeth is broadened and the forward edge of the symphysis is wide.

Wood bison Bison bison athabascae (Rhoads, 1897)

All the features characteristic of B. bison athabascae indicate that it is closely related to the extinct forms of the Pleistocene and earlier Holocene species B. cesaris (=B. priscus). I am, for the time being, leaving it as the subspecies B. bison, but it is probable that in future it will have to be considered as a representative of B. cesaris which has survived to the present day. B. athabascae, like Ovibos, lives in areas which have retained conditions resembling those of the Pleistocene and early Holocene. In Canada and Greenland Ovibos encounters terrain associated with the presence of continental ice. The wood bison inhabits the region around Great Slave Lake, where, in the forest, under harsh climatic conditions, there are small steppe sectors evidently similar to the cold forest steppes which were widespread in Siberia and Canada at the end of the Pleistocene and in the early Holocene.

The wood bison, like the musk-ox, is a "live fossil" - a contemporary of the mammoth which has survived to the present day.

Type. An adult male killed by Indians within 50 miles southwest of Fort Resolution, Northwest Territories, Canada, probably in March 1892. Donated by W. Pike. National Museum of Canada, No. 299, Accession No. 92 - 1.

Description. Skull. Very large; the greatest length is 560 to 600 mm, averaging 575 mm; the width of the forehead behind the orbits is 270 to 315 mm and averages 290 mm; the width along the rear walls of the orbits is 325 to 385 mm and averages 355 mm. The skull is long and very broad. The forward ends of the intermaxillaria have no blade-shaped protuberances on their forward outer edge. The muzzle is not widened in front, but rather rounded, similar to B. cesaris, and the upper edges of the forward nasal entrance are almost parallel, as in B. cesaris. The nasal bones narrow comparatively slightly in the shape of a wedge towards the front; there is little difference in the width of the forward and rear sections, which can be almost straight, again as in B. cesaris. There is in most cases a depression on the forehead behind the nasal bones. The horn shafts are long - longer than in all other present and

recently extinct forms from northeastern Siberia. The distance between their tips varies from 585 to 740 mm and averages 665 mm. The horn shafts are recurved slightly downwards; their tips are situated above the frontal surface. The shafts are very thick: their diameter at the crown varies from 80 to 110 mm and averages 95 mm. Their bases are moderately prolapsed; hence the distance between them and the external auditory opening is approximately equal to or slightly more than the vertical diameter of the foramen magnum. The horns are slightly spiral; their tips are bent in and up. The sulcus supraorbitalis branches onto the orbital "socket". The lacrymal bones are for the most part excised in front and form a narrow tooth projecting forward, as in B. cesaris. There is a weakly defined preorbital depression. The pharyngeal protuberances are corrugated and very large and long; they form crests and processes, project forwards, and enter the choana much further than the allae magnae. The musculus longus capitis is very well developed because of the very heavy head and horns. The choana is somewhat wider than in B. bison bison. The forward ends of the occipital condyles approach each other in front of the foramen magnum; the distance between them is about 8 mm. The system of incisor-like teeth is narrower than in B. bison bison and similar to that in B. cesaris and B. bonasus.

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